OVIPOSITION AND HOST FEEDING BEHAVIOR OF
APHELINUS ASYCHIS (HYMENOPTERA: CHALCIDOIDEA: APHELINIDAE) ON *SCHIZAPHIS GRAMINUM* (HOMOPTERA: APHIDIDAE) AND SOME REACTIONS OF APHIDS TO THIS PARASITE

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Abstract.—Fifty-four *Aphelinus asychis* (Walker) were observed during their first encounters and ovipositional attacks with unparasitized *Schizaphis graminum* (Rondani). Oviposition occurred when wasps inserted their ovipositors in aphids for at least 60 s, and aphids were not paralyzed prior to or during ovipositor insertion. Before leaving aphids, 65% of the wasps made single ovipositor eversions (SE's), 35% made multiple ovipositor eversions (ME's). Everted ovipositors did not always pierce aphids. Single eversions (as opposed to ME's) preceded oviposition in 75.7% of 33 observations. Durations of ovipositor eversions which preceded oviposition were significantly longer than durations of eversions that did not precede oviposition. Twenty wasps were observed host feeding. Prior to feeding, wasps stung and paralyzed aphids. Oviposition and host feeding were discrete activities always carried out on separate aphids. Wasps' initial approaches and attacks on aphids, however, were similar in both types of attack. Wasps took significantly longer to sting aphids than to oviposit. Aphid reactions to wasps included body jerking, antennating, walking away and kicking with one leg. Aphids reacted violently to stinging and some ovipositional attacks. Alarm behavior in some aphid groups occurred.

This study was conducted in an attempt to identify behaviors involved in oviposition and host feeding of a hymenopterous parasite, *Aphelinus asychis* (Walker), on the greenbug, *Schizaphis graminum* (Rondani). In addition, some reactions of aphids to wasp presence and attacks were noted.

Aphelinus asychis was first introduced into the United States in 1968 to help control *Schizaphis graminum* which was first found in the United States in 1882 and presently causes millions of dollars damage annually to grain crops, e.g., *Sorghum vulgare* (Pers.).

Although *Aphelinus asychis* is a potentially valuable biocontrol agent against *Schizaphis graminum*, there has never been a detailed study of its oviposition and host feeding behavior. The only descriptions of host feeding (Esmaili and Wilde, 1972; Cate et al., 1973) are brief, lack detail as to the frequency of various behaviors and are inconsistent as to the

duration of ovipositor insertion. Oviposition by *A. asychis* has been observed (Rogers, 1976) but never described in detail.

Materials and Methods

Sorghum vulgare was grown in 355 cm³ plastic pots in a greenhouse. When about 10 cm tall, plants were transferred to a separate area and infested with *Schizaphis graminum*.

Pots with about 4 plants and 10 aphids per plant were transferred to the laboratory and placed in 42,000 cm³ terraria. Each terrarium held 26–32 pots. Terraria were fitted with clear plexiglass tops, each with 2 ventilation holes covered with nylon mesh and 1 access hole with a 60 cm long nylon mesh sleeve which was tied closed when not in use. Several *Aphelinus asychis* were placed in some terraria and allowed to feed on and parasitize aphids. All terraria were kept under plant-growth fluorescent bulbs for 12 h per day. Laboratory temperature was from 20.0–26.5°C.

Gelatin capsules (no. 1) were used to capture and carry individual adult wasps and to isolate and hold individual mummies. This reduced or eliminated possible injury to wasps which frequently occurs when using a camel's hair brush.

A total of 54 wasps was observed for 1 h each at about 24°C. To observe oviposition and host feeding of *A. asychis* on *S. graminum*, a blade of *Sorghum*, with a minimum of three feeding aphids, was placed in a plastic petri dish; one *A. asychis* female was also placed in the dish which was then covered. Observations were made through a dissecting microscope. All aphids used for observations were taken from unparasitized cultures. This method is similar to that of Goff and Nault (1974).

Behavior that was observed included oviposition host feeding and reactions of aphids to the presence of and attacks by wasps. Attacks were timed with a stopwatch from the moment the wasp turned and everted her ovipositor to the moment she retracted it.

In addition, 16 aphids were dissected to determine whether oviposition actually took place when a wasp's ovipositor pierced the aphid. Five aphids were dissected after having been fed on to determine whether oviposition occurred.

In reporting results, the symbol $\bar{x}$ is used to denote a mean; M, median; *TEP* test for the equality of two percentages (Sokal and Rohlf, 1969); *MWUT*, Mann-Whitney U-test; and *WMPT*, Wilcoxon's matched pair test. All numerical data are based on randomly-selected animals and observations.

Results and Discussion

Ovipositional attacks.—In "typical" ovipositional attacks, *Aphelinus asychis* walked on substrates and tapped surfaces with extended antennae.

On encountering *Schizaphis graminum* by touching or coming within about 1 cm of them, wasps either retreated or stopped and withdrew antennae, leaving only flagellae slightly extended and quivering. If aphids were not within ovipositor reach, wasps slowly approached and antennated them with only flagellae extended.

When they were sufficiently close to aphids, wasps began to "sway," rocking their bodies from side to side. Occasionally, swaying was interrupted several times for a few seconds each time while wasps lowered antennae and remained motionless. Swaying was occasionally accompanied by wasps' grooming their metasomas with hind legs, grooming hind legs with middle legs or both. Wasps also either turned their heads slightly from side to side or kept them still.

After approaching and facing aphids, wasps rapidly turned about 180° to the left or right, everted ovipositors and stabbed at aphids. If ovipositors did not make immediate contact with aphids, wasps usually made one or more stabbing attempts.

When ovipositors pierced aphids, wasps stood motionless and kept antennae lowered for the duration of ovipositor insertion (Fig. 1). Occasionally, wasps made slight thrusts with ovipositors.

Oviposition occurred when everted ovipositors pierced and were inserted in aphids for at least 60 s; this was determined by dissecting 16 aphids immediately after ovipositional attacks in which everted ovipositors were in aphids from 4–542 s. Immediately before retracting ovipositors, wasps raised heads and extended antennae slightly. After wasps oviposited and retracted ovipositors, they retreated.

Although there are no other published descriptions of oviposition for *Aphelinus asychis*, several aspects of this behavior are similar to those reported for other parasitic hymenopterans. Observations suggest that *A. asychis* usually touches or is within 1 cm of aphids before attacks are initiated. Messenger (1967), reported that *Praon exsoletum* (Nees) detected hosts only after actually contacting them with antennae, and he concluded that the wasp's distance perception was limited. Similar observations have been made with *Lysephlebus testaceipes* (Cresson) (Webster and Phillips, 1912), *Tetrastichus flavigaster* Brothers and Moran (Moran et al., 1969) and *Aphelinus flavus* Thompson (Hamilton, 1973). As in most *A. asychis* observed in this study, females of each of the above species appeared to encounter hosts during apparently "nondirected" wanderings and react to hosts after contact.

Wasps probably gain sensory information as to host suitability and appropriateness of ovipositor insertion sites when they antennate aphids and sway prior to ovipositor eversion. Webster and Phillips (1912) observed *A. nigritus* Howard approach, antennate, and sway in front of *Schizaphis graminum* in a manner similar to that of *Aphelinus asychis*. Antennation of hosts prior to ovipositor eversion has also been reported for

Fig. 1.   Everted ovipositor of *Aphelinus asychis* female piercing *Schizaphis graminum.*

A. *mytilaspidis* (Marchal, 1909), *Praon aguti* Smith, *Lysephlebus testaceipes* (Sekhar, 1957), *Tetrastichus flavigaster* (Moran et al., 1969), and *Aphelinus flavus* (Hamilton, 1973). Moran et al., (1969) presumed that antennation functions in olfactory identification of the host by the wasp. Chalcidoid antennae have sense organs necessary for host finding, according to Askew (1971). After their ovipositors are inserted into hosts, sense organs located on ovipositors probably supply additional information to wasps concerning host suitability (Moran et al., 1969; Askew, 1971).

The following results, except where otherwise indicated, are based on the first observed ovipositor eversions, either single or multiple, which each of 54 wasps made with a different, unparasitized aphid.

When attacking aphids, wasps exhibited either single ovipositor eversions (SE's) or multiple ovipositor eversions (ME's); ME's were comprised of from 2–14 eversions. Everted ovipositors did not always pierce or even contact aphids, and piercing was not always followed by oviposition. In SE's which they made after approaching aphids, wasps turned about 180° away from aphids, everted and retracted ovipositors once, and retreated. In ME's, wasps turned 180° away from aphids, everted and re-

tracted ovipositors, turned 180° to face aphids, turned 180° again, everted and retracted ovipositors a second time; this sequence of 3 turns was repeated from 3–14 times before wasps retreated. Figure 2 shows sequences of behaviors displayed during first encounters of 54 *A. asychis* with 54 *Schizaphis graminum* during 1 h observation periods.

Single ovipositor eversions, as opposed to ME's, occurred 64.8% of the time, and SE's preceded oviposition in 75.7% of 33 observations. This suggests that *Aphelinus asychis* budgeted time and energy efficiently in that they usually pierced *Schizaphis graminum* only once before ovipositing. Wasps that pierced aphids several times before ovipositing may have been attempting to gain additional information as to whether or not aphids were already parasitized, to place their ovipositors in more favorable sites within aphids, or both. Wasps that pierced aphids but failed to oviposit may have received stimuli indicating that aphids were unsuitable for parasitization. If this is the case, evaluation and rejection of unsuitable hosts could be accomplished in a relatively brief time of 2 to about 59 s.

Of the total time spent in everting ovipositors, 35 wasps spent 94.0% of this time in SE's preceding oviposition; 19 wasps spent 51.6% of this time in ME's preceding oviposition. There is a significant difference between these groups ($p = 0.0003$, *TEP*). In SE's, wasps pierced, presumably evaluated the suitability of aphids and oviposited in significantly less total time than in ME's.

Praon exsoletum exhibits similar behavior. In studying its daily ovipositional pattern, Messenger (1967) found that *P. exsoletum* oviposited from 18–24 times in 20–30 min, making one ovipositor insertion per aphid. After a period of rapid ovipositing, however, wasps repeatedly struck at aphids before ovipositing. As in *Aphelinus asychis*, these ME's consumed more time and preceded fewer ovipositions than SE's. A study to determine the daily ovipositional pattern of *A. asychis* could be helpful.

Durations of SE's which preceded oviposition were not significantly different from durations of the last eversion of ME's which preceded oviposition ($U = 94$, $p > 0.05$, $N_1 = 20$, $N_2 = 8$, *MWUT*). Nor were SE's which did not precede oviposition significantly different from durations of ME's which did not precede oviposition ($U = 58$, $p > 0.05$, $N_1 = 10$, $N_2 = 11$, *MWUT*).

Durations of SE's which preceded oviposition were significantly longer than durations of SE's which did not precede oviposition ($U = 198$, $p < 0.002$, $N_1 = 20$, $N_2 = 10$, *MWUT*). Durations of ME's which preceded oviposition were also significantly longer than durations of ME's which did not precede oviposition ($U = 88$, $p < 0.001$, $N_1 = 11$, $N_2 = 8$, *MWUT*).

Wasps made initial approaches to aphids from the front, rear or either side. In ME's, wasps made each ovipositor eversion from the same position relative to the aphid. Rear approaches seemed to precede oviposition more
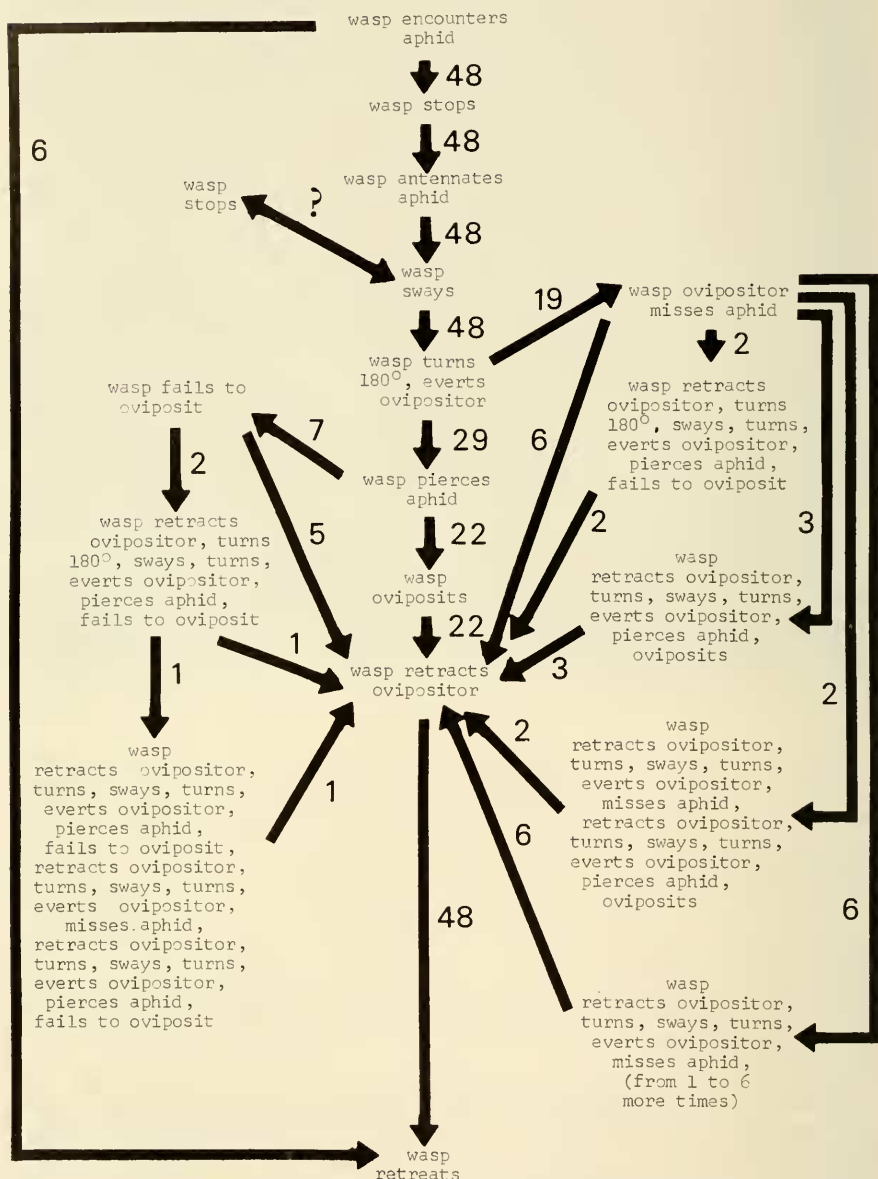
Fig. 2. Behaviors exhibited during first encounters of 54 different *Aphelinus asychis* with 54 different *Schizaphis graminum*. Numbers by arrows indicate frequencies of changes from one behavior (or sequence of behaviors) to another. Question mark indicates that frequency was not noted. See text for further explanation.

often than front or lateral approaches, but sample sizes were too small to allow statistical analysis.

Twenty-six wasps were observed for the direction of turn immediately prior to everting ovipositors in SE's and ME's. In ME's, as noted above, wasps turned about 180° to face aphids after retracting ovipositors, and then they turned again immediately prior to everting ovipositors. They did this two or more times. Turns made immediately prior to ovipositor eversion were in the alternate direction (e.g., right, left or left, right) to the previous turn prior to ovipositor eversion in 53.8% of the cases; 46.1% of such turns were in the same direction (e.g., right, right or left, left) as the previous turn observed. There was no significant difference in turning direction compared to a hypothetical turning of either right or left 50.0% of the time $(0.9 > p > 0.5,$ TEP).

Stinging and host feeding.—Host feeding is common among chalcidoids and represents an example of economy in time and effort, in that individual hosts provide food for both adults and progeny (Askew, 1971). Esmaili and Wilde (1972) and Cate et al. (1973) found that host feeding by newly emerged *A. asychis* almost always preceded oviposition.

Nutrients obtained from host feeding by *Aphelinus* and other genera are probably necessary for oogenesis (DeBach, 1943; Moran et al., 1969; Askew, 1971). Oogenesis occurs throughout the adult life of *A. semiflavus* (Howard) (Schlinger and Hall, 1959) as it probably does in *A. asychis*. Therefore, periodic host feeding is probably necessary to obtain nutrients for continuous oogenesis.

Twenty *A. asychis* were observed feeding on 20 different, unparasitized *Schizaphis graminum*. Wasps stung and paralyzed aphids, then they fed from wounds made by ovipositors.

Stinging attacks were initially indistinguishable from ovipositional attacks. Wasps approached and antennated aphids, swayed, turned, everted ovipositors and pierced aphids in apparently the same manner as in ovipositional attacks. Wasps presumably injected, through their ovipositors, a paralyzing agent into aphids.

The first noticeable difference in wasp behavior during stinging attacks, as compared to ovipositional attacks, occurred after aphids were effectively paralyzed and their movements merely uncoordinated leg waving. Wasps (with their ovipositors still inserted in aphids) usually backed up slightly and stood with their hind legs on aphids. Wasps remained in this position, motionless, except for occasional thrusts of ovipositors and with antennae lowered, for several more minutes.

As in ovipositional attacks, immediately prior to retracting ovipositors, wasps raised their heads and slightly extended their antennae. Wasps then immediately made another stinging attack on the same aphids or an-

temnated aphids to locate wounds made by ovipositors. If they did not locate wounds, wasps made additional stinging attacks, usually of shorter duration than the first ones.

When wasps found wounds, they antennated them for several seconds, then positioned their heads over wounds, lowered their bodies and fed. Feeding continued for several minutes and usually took longer than stinging. Wasps either fed once and retreated or alternately stung and fed from the same aphid before retreating.

Figure 3 shows the behavioral sequence of stinging attacks and feeding by 20 *Aphelinus asychis* on 20 *Schizaphis graminum*. This sequence begins with wasp ovipositor insertion into aphids; behavioral sequences occurring before this are similar to those for ovipositional attacks.

Initial approach to and attack of hosts is similar for both oviposition and stinging in *Aphelinus asychis*, *A. flavus* (Hamilton, 1973), *A. semiflavus* (Schlinger and Hall, 1959), *A. mytilaspidis* (Marchal, 1909) and *Tetrastichus flavigaster* (Moran et al., 1969). In our study, after initiation of stinging attacks by *Aphelinus asychis*, the first noticeable difference in behavior compared to ovipositional attacks was their placing hind legs on aphids. This has also been observed by Esmaili and Wilde (1972). The function of this behavior has not been studied, but it might allow wasps to thrust ovipositors deeper into aphids.

Paralyzing aphids by *A. asychis* prior to their feeding probably facilitates this activity. Unparalyzed aphids would not be likely to remain still while wasps fed at their wounds.

Wasps were never observed paralyzing aphids in which they had oviposited, nor has this been reported in the literature for *A. asychis*. Parasitized aphids remain alive and mobile for several days before mummification and thus provide one means for wasp dispersal.

Of the 20 wasps observed host feeding, 11 approached aphids from the front, 7 approached from the rear and 2 approached from the sides of aphids. All subsequent stinging attacks and feeding were made from the approach position. In their first stinging attacks on aphids, 10 wasps turned to the right and 10 turned to the left prior to ovipositor eversion.

In attacks by 18 wasps, durations from the beginning of the initial paralyzing sting to when wasps placed hind legs on aphids were from 210–570 s ($\bar{x} = 330$, $M = 390$). Esmaili and Wilde (1972) reported durations of from 120–180 s for this activity. Wasp hind leg placement on aphids always occurred after their paralysis.

Durations of initial paralyzing stings, before wasps either began feeding or attempted to find sites of ovipositor insertion, were from 277–1,399 s ($\bar{x} = 598$, $M = 838$, $N = 20$). These durations were significantly longer than durations of SE's which preceded oviposition ($U = 395$, $n_1 = 20$, $n_2 = 20$, $p < 0.001$, MWUT). Thus, wasps took significantly longer to para-
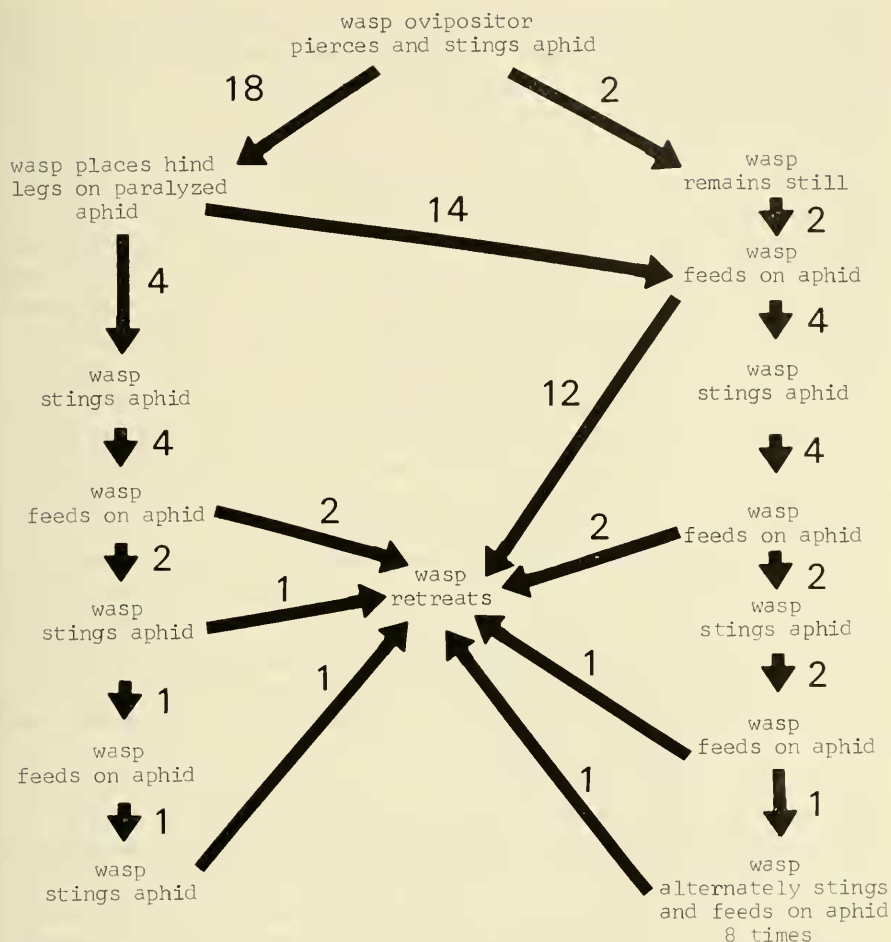
Fig. 3. Behaviors exhibited during first encounters of 20 different *Aphelinus asychis* with 20 different *Schizaphis graminum* during wasp stinging and feeding attacks on aphids. Numbers by arrows indicate frequencies of changes from one behavior (or sequences of behaviors) to another. See text for further explanation.

lyze aphids than to oviposit. Cate et al. (1973) reported that the initial sting of *A. asychis* lasted from 300–7,200 s, a much wider range than observed in our study. Hamilton (1973) reported that the average duration for stinging by *A. flavus* is 380 s.

After the initial paralyzing sting, most wasps fed and then retreated. Eight wasps, however, stung aphids one or more times after either feeding or being unsuccessful in finding sites of ovipositor insertion; these wasps alternated stinging attacks with feeding. These subsequent stinging attacks

on the same aphids lasted from 39–821 s ($\bar{x} = 399$, $M = 330$). Statistical analysis suggests that initial stings were longer than subsequent stings ($T = 6$, $N = 8$, $p = 0.055$, $WMPT$). The average duration of all stinging attacks, both initial and subsequent, was 757 s.

Repeated and alternating stinging and feeding has been reported for *A. asychis* (Cate et al., 1973), *A. mytilaspidis* and *Tetrastichus xanthomelaenea* (Rond.) (Marchal, 1905). Initial stings made by *A. asychis* on aphids seemed to be sufficient to paralyze them and were significantly longer than subsequent stings on the same aphids. Marchal (1905) and Cate et al. (1973) also noted that repeated stings were often quite brief. Subsequent stings might serve to open other wounds in aphids or to enlarge existing wounds rather than to inject paralyzing agent into aphids.

Wasp initial feedings lasted from 141–1,815 s ($\bar{x} = 680$, $M = 978$, $N = 20$). Durations of subsequent feedings by 5 wasps were from 12–2,916 s ($\bar{x} = 1,083$, $M = 1,464$). The average duration of all feedings was 952 s. There was no statistical difference between durations of all stinging attacks and all feedings ($T = 83$, $N = 20$, $p > 0.05$, $WMPT$).

The paralyzing agent injected by wasps seemed to cause a number of changes in the appearance and behavior of stung aphids. These changes began to occur several minutes after ovipositor insertion. Usually, aphid abdomens swelled and raised, causing the aphid hind legs and occasionally the middle legs to be lifted off substrates. Hind legs waved in a weak, uncoordinated manner in the air. Waving became progressively slower and weaker until it eventually stopped.

At the same time, aphid antennae, which were usually held against dorsums, raised slightly and extended at various angles to aphid bodies. Aphids were usually prevented from falling by keeping their stylets embedded in *Sorghum* blades. In general, paralyzed aphids appeared completely to lose control of their movements, and they became immobilized and defenseless. Esmaili and Wilde (1972) reported similar changes in the appearance and activity of paralyzed *Schizaphis graminum*.

While wasps were feeding, aphid color changed from the usual green to yellow-green to yellow and finally to brown, a process which took from 20–45 min. The paralyzing agent, or substances introduced during wasps' feeding or both, might bring about this gradual color change, which was also noted by Cate et al. (1973) in the same host. When wasps finished feeding, aphids were shriveled and shrunken.

Wasps often had dark, flattened abdomens prior to host feeding. During feeding, however, abdomens swelled and became rounded and honey-colored. This process roughly corresponded to the gradual shriveling of aphids.

Dissection of 5 aphids that were fed upon *Aphelinus asychis* did not

reveal any eggs deposited by wasps. Marchal (1909) and Esmaili and Wilde (1972) reported similar findings and stated that host feeding renders hosts unsuitable for oviposition. Full larval development of *A. asychis* in the dried, shrunken remains of fed-on aphids would seem difficult.

Aphid reaction to wasps.—Aphids reacted in a variety of ways and seemed to have some effective defense mechanisms against wasps. The most conspicuous defense reaction by aphids was "jerking." Aphids, with stylets embedded in *Sorghum* blades, quickly and forcefully flipped up their abdomens and lifted their hind and middle legs off the substrate. This was often done continuously for several minutes. Almost always, after one aphid began jerking, nearby aphids would also begin. A *Sorghum* blade often had several small groups of aphids in constant movement of this kind.

Other reactions of aphids included quickly extending antennae forward to touch wasps, crawling away from wasps and striking with legs at wasps.

Jerking, antennating, crawling away and kicking have been reported for several aphid species, including *Schizaphis graminum*, by Webster and Phillips (1912) and Hamilton (1973). These reactions seemed to have varying degrees of effectiveness as defense mechanisms depending on how soon they were initiated.

Jerking by *S. graminum* seemed to prevent attacks when it was initiated before or soon after wasps approached. Other aphids jerked after one started and this probably helped these other aphids from being attacked. This type of behavior was also noted by Hight et al. (1972).

Wasps apparently required or preferred stationary hosts, as they were never observed initiating attacks on aphids that were not still when they were approached. Jerking by aphids before wasps inserted ovipositors was usually effective in preventing contact because wasps seldom hit moving aphids with their ovipositors.

Aphid defense behaviors seemed to be stimulated by various kinds of wasp activity. On 5 occasions, groups of several aphids antennated a wasp and began jerking when the wasp walked past the aphids, they did not touch or give any noticeable indication of attacking them. On 29 occasions, wasps, which approached aphids and appeared about to attack them, seemed to provoke reactions from aphids which seemed to cause wasps to retreat without attacking. These reactions were all of the types mentioned above.

Although many aphids showed no noticeable reaction to ovipositional attacks, some aphids jerked strenuously after being pierced. Once jerking was initiated, it usually continued for several minutes, even after wasps retreated. Jerking after wasps inserted ovipositors seemed to have little or no effect on the outcome of the attacks, either ovipositional or stinging

attacks. Aphids often completely lifted wasps off the substrate, but wasp ovipositors remained in the aphids and wasps remained as still as possible, never raising antennae until just prior to retracting ovipositors.

The most violent and prolonged reactions by aphids were caused by wasp stinging attacks. In every stinging attack observed, aphids began jerking violently within from 2–5 min after ovipositor insertion. Aphids continued violent, strenuous movement for several minutes until they gradually began to show signs of paralysis. Frequently, aphids twisted around, using their stylets embedded in *Sorghum* as pivots. In 8 stinging attacks, aphids removed stylets from *Sorghum* and rapidly walked away, dragging wasps with them. Wasps were never dislodged by these activities, although they were often dragged several centimeters or flipped over.

Alarm behavior was observed during 4 stinging attacks; immediately after a stung aphid began jerking, all nearby aphids withdrew their stylets from *Sorghum* and quickly scattered. On 3 occasions, stung aphids jerked violently and produced yellowish droplets from the tips of both cornicles, after which all nearby aphids began jerking and then scattered. An alarm pheromone in the cornicle secretions of *Schizaphis graminum* and other aphids was demonstrated by Bowers et al. (1972) who identified the active substance as trans-B-farnesene. Kislow and Edwards (1972) noted interspecific reactions to the pheromone which is detected by sensoria located on aphid antennae (Nault et al., 1973). Aphid cornicle secretion is considered a self-serving and altruistic defensive system by Nault et al. (1976).

One wasp placed her right foreleg in a cornicle droplet while she was feeding, and the droplet apparently hardened around her leg. The wasp struggled for about 45 min before freeing herself. This has also been noted by Edwards (1966) who found cornicle secretions to be lipid droplets in water that rapidly crystallizes when in contact with a solid surface. Edwards (1966) found only 2 wasps entrapped in secretions produced by several thousand aphids; Goff and Nault (1974) never observed wasps entrapped by cornicle secretions. Our study also suggests that cornicle secretions rarely entrap wasps.

Schizaphis graminum probably detect approaching *Aphelinus asychis* partly through vision. Dixon (1958; 1973) stated that aphids would be at an advantage when predators approached from the front because they could be seen more easily. This study supports Dixon's supposition because although more wasps approached aphids from the front, frontally approached aphids often reacted defensively, and a larger percentage of rear approaches preceded oviposition.

Schizaphis graminum probably also use tactile perception to detect wasps. Aphids which did not show any other reaction to wasp often jerked only after wasps pierced them. This did not seem to affect the outcome of the attacks, but it often caused nearby aphids to begin jerking.

Additional observations.—Two variations of behavior associated with ovipositional attacks were occasionally observed. Five wasps approached single aphids, stopped and briefly antennated them. Then, instead of swaying, they lowered their antennae and quickly butted the fronts of their heads against the aphids. Two wasps butted aphids once, and 3 wasps made 2 such charges in rapid succession. All wasps then continued with the usually observed sequence of turning, everting ovipositors and stabbing at aphids. Wasps exhibiting this type of behavior appeared to move more quickly and to take less time antennating aphids than other wasps, and in general, appeared more agitated than usual.

Five other wasps "attacked" either cast skins of aphids (2 wasps), aphid eggs (2 wasps) or a spot on a *Sorghum* blade where an aphid had recently been feeding (1 wasp). In all cases, the wasps showed the usual behavioral sequence prior to ovipositor eversion. One wasp made a SE and then retreated. All others made from 3–14 eversions before retreating.

Factors that initiate attacks probably includes wasps' motivation to either oviposit or feed and stimuli from aphids, e.g., odors, sizes, shapes. Wasps that are highly motivated to attack probably do so at lower stimulus thresholds than wasps that are less highly motivated (Sekhar, 1957). This may explain wasp attacks on aphid skins, eggs and a recently vacated feeding site. Each of these objects may have carried sufficient aphid odor, had other characteristics or both, to stimulate highly motivated wasps to attack. Similar wasp behavior has been reported for *Aphelinus nigritus* (Webster and Phillips, 1912) and *Tetrastichus flavigaster* (Moran et al., 1969).

Wasps butting their heads against aphids rather than swaying prior to turning and everting ovipositors might also be a reflection of the motivational state of the wasps. Swaying often consumed several seconds and, as noted, was often interrupted several times while wasps remained motionless. Wasps that are highly motivated to attack may have eliminated this relatively time-consuming behavior and replaced it with a far more rapid action.

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